Tree of the sea

Witbaard, Rob

CHAPTER 7*

A long-term growth record derived from *Arctica islandica* (Mollusca, Bivalvia) from the Fladen Ground (northern North Sea)

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ABSTRACT

Long-term variations in shell growth of the mollusc *Arctica islandica* (Mollusca, Bivalvia) from the northern North Sea have been assessed retrospectively by using the annually deposited internal growth lines. Relatively young specimens yielded a detailed year-to-year chronology while the growth record of specimens older than 30 years yielded time series with a length exceeding 100 years. The long-term growth trends demonstrated a marked alternating sequence of periods in which growth was below and above expectation. A 33-year long cycle could be discerned. Since the 1960s the growth patterns in *Arctica* from two nearby locations were opposite, while they resembled each other in the period before 1960.

Although expected, no significant correlations were found between shell growth and local bottom water temperature or CPR phytoplankton variables. The alternative hypothesis to explain the variations in shell growth is the existence of a link between local hydrographical phenomena and the occurrence of the *Arctica* beds. The stations from where the specimens were collected were discovered when a drogue was caught by a local eddy. It is speculated that this distribution pattern is the consequence of import and accumulation of organic matter by the eddy system. This idea is supported by the correlation between the variations in the influx of North Atlantic water into the North Sea which determines the existence of the eddy.

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INTRODUCTION

The scarcity of long-term data on offshore marine benthos is regrettable since the benthic community can be seen as a time-integrated response to the ambient environmental conditions. Changes in these conditions are likely to affect both the community structure and certain attributes of their members, such as reproduction and growth. In species with skeletal parts, annual growth can often be recognised by the rhythmic deposition of the hard structures. This feature enables a retrospective analysis of growth variations of the organisms in question, analogous to trees (Jones, 1983). However, the lifespan of most subtidal invertebrates (<10 years) in combination with the inaccuracy in ageing sub-fossil material hamper in most cases the construction of reliable long-term series covering the past century.

In this respect, the bivalve mollusc *Arctica islandica* is of special interest because it complies with four criteria proposed by Thompson & Jones (1977) that should be met in order to make a species useful:

1: Specimens from one population demonstrate synchronised growth variations (Thompson *et al*., 1980; Witbaard & Duineveld, 1990).
2: The species has a consistent annual formation of growth lines, even in the oldest individuals (Turekian *et al*., 1982; Thompson *et al*., 1980; Ropes, 1988; Witbaard *et al*., 1994).
3: It has a great longevity. Ages of 100 years are common in most populations (Ropes, 1985; Witbaard & Duineveld, 1990).
4: Growth is continuous throughout life which can be concluded from the fact that the oldest animals still deposit annual growth lines (Thompson *et al*., 1980; Ropes *et al*., 1984).

In the present study, temporal growth variations in two dense patches of *Arctica islandica* in the Fladen Ground (northern North Sea) are described by methods originating from dendrochronology and adopted by sclerochronology (Jones, 1983). We focussed on this particular population because it originates from an area which is under direct influence of the Atlantic Ocean. The water depth in the Fladen Ground shelters the population from erratic short-term disturbances like storms or abrupt temperature changes. Hence, growth variations in the local *Arctica islandica* population are assumed to reflect important changes in the water column processes (*e.g.* primary production or sedimentation rates). In order to test this hypothesis, the ensuing growth patterns were correlated with environmental data such as CPR phytocolour and annual and monthly abundance of diatoms and dinoflagellates.

METHODS

Site description

The Fladen Ground is located about 100 miles north-east off Aberdeen (Scotland). The bottom consists of an irregular pattern of glacial depressions between 100 and 150 meter depth (Basford & Eleftheriou, 1988). The area is located just south of the major water inflows from the Atlantic Ocean into the northern North Sea (figure 7.1). The central and deeper parts of the area lie in the centre of an only recently recognised, semi-permanent, topographically steered cyclonic eddy formed by the "Fair Isle Current" and the "East Shetland Atlantic Inflow" (Turrell, 1992a; 1992b; Svendsen *et al.*, 1991).

Figure 7.1

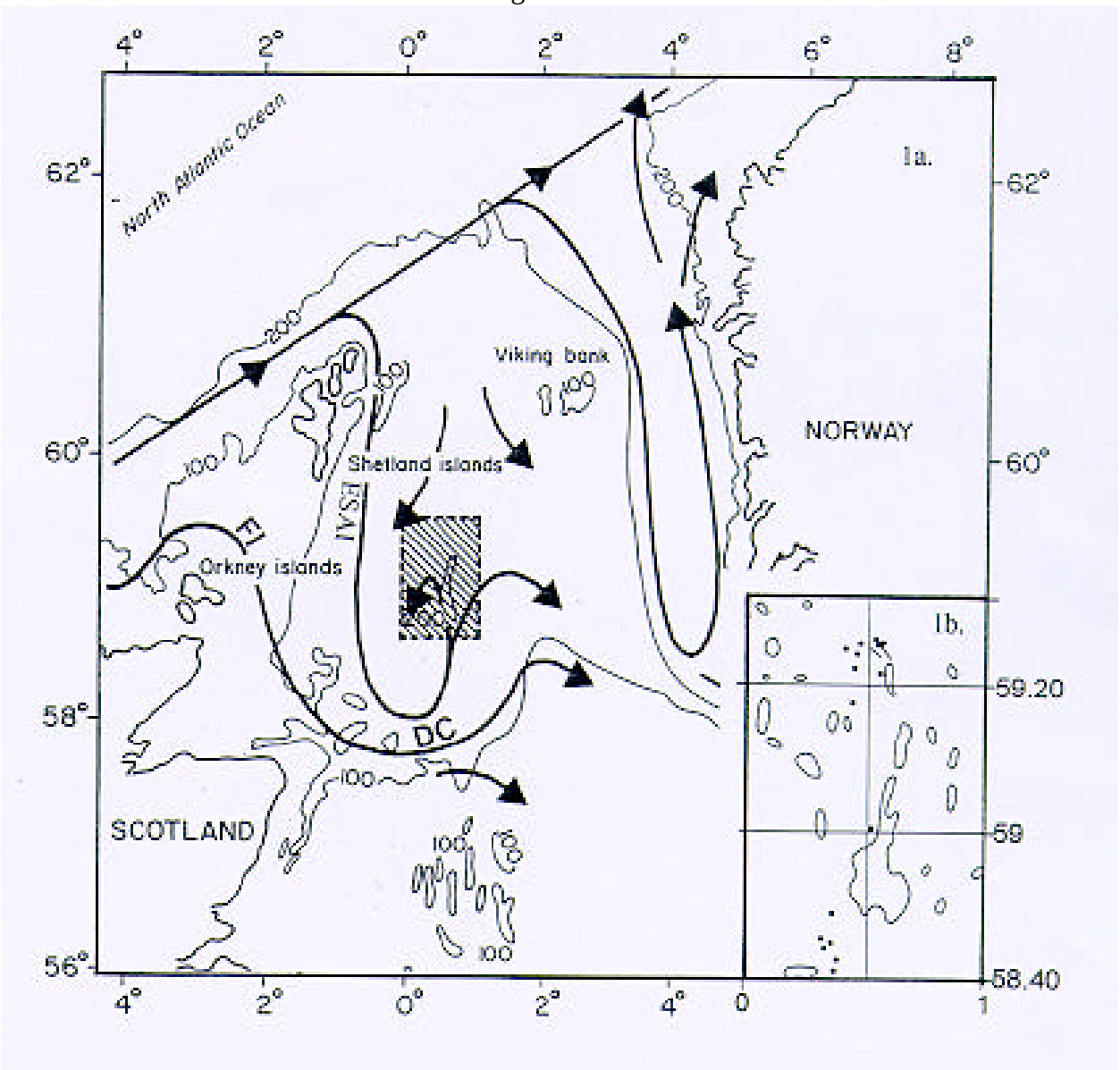

Figure 7.1. Map showing the northern North Sea with main circulation patterns (after Turrell, 1992a, 1992b). FI, Fair isle current; DC, Dooley current; ESAI, East Shetland Atlantic Inflow. The hatched area represents the REFLEX box as studied by Wilde *et al*. (1986). The inset gives the sampling locations within the REFLEX box. •, stations sampled by Wilde *et al*. (1986); \ = trawl tracks taken in December 1991.

In summer the area is thermally stratified with a thermocline between 30 and 70 meter (McIntyre, 1961). This thermocline traps a bell of cold water in the central parts of the area, resulting in a seasonal temperature variation of the bottom water between 5.7 and 7.8°C (Faubel *et al*., 1983). Year to year variations of the bottom temperature in summer are even smaller and cover the range between 5.9-7.3°C (Ellet & Blindheim, 1992). Stratification lasts until the end of summer. A major part of the primary production takes place in April and May and the net annual primary production ranges between 57 and 100 gr.C.m^{-2} (Steele, 1956; 1974; Fransz & Gieskes, 1984). The benthic fauna of the area has been described in a series of papers (McIntyre, 1961; Faubel *et al*., 1983; Hartwig *et al*., 1983; Wilde *et al*., 1986; Eleftheriou & Basford, 1989; Basford & Eleftheriou, 1988 and Basford *et al*., 1989). Wilde *et al*. (1986) was, however, the first who reported high numbers of *Arctica islandica* in the area, *viz.* 16 ind.m^{-2} accounting for up to 75% to the total ash-free dry weight biomass. Trawl surveys in the northern North Sea by Basford *et al*. (1989) substantiated that these high densities are restricted to a few small patches, which explains why they were not found in other studies (Hartwig *et al*., 1983; McIntyre, 1961).

Collecting and ageing

Three batches of living *Arctica* were collected in the Fladen Ground on two occasions. The first two batches were recovered during the REFLEX expedition in spring 1983 by Wilde *et al*. (1986). The positions of the benthic stations sampled during this expedition were determined by the position of a drogue buoy which was followed (Mulder & Manuels, 1982). This resulted in two station clusters, one to the south (58°45'N 0°20'E) and the other to the north (59°25'N 0°30'E) (see inset in figure 7.1). The third batch of *Arctica* was collected in December 1991 when the northern location was resampled with a beam trawl during a cruise with RV. Pelagia. Table 7.1 summarises the origin and date of collection of all 62 shells used for this study.

Acetate peel replica of *Arctica* shell cross-sections were used to make growth line measurements. All acetate peels were made of left-hand valves in accordance with Ropes (1985, 1988). Of each individual shell two or three different, but parallel cross-sections and peels were made. The widths of the growth increments in the peels were measured under 30-125 X magnification with a Zeiss compound microscope equipped with ocular micrometer and a Sony CCD video camera (XC77CE) plus video printer (Sony, UP860CE). In young specimens, measurements were made of the hinge-band, while in older specimens, they were made of the valve proper. Each growth increment was assigned to a particular year starting from the edge of the shell resulting in a time series of increment widths.

Table 7.1

Station	Lat.	Long.	Depth (m)	Young	Old
South 1983	58°45'N	0°20'E	120-140	11	4
North 1983	59°25'N	0°30'E	120-180	6	5
North 1991	59°25'N	0°30'E	120-180	18	18
Total				35	27

Table 7.1. Summary of sampling details. Location, depth and the number of young and old shells from each location is given. Young shells have shell heights between 20 and 50 mm. The age of the young shells varies between 10 and 30 years.

Chronologies of growth variations

Because of the bimodal age distribution of the *Arctica* samples and the non-linear ontogenetic growth of the species (Witbaard & Duineveld, 1990), groups of young clams (≤ 30 years; shell height ≤ 50 mm) and old clams (> 30 years) were treated separately.

The synchrony of year-to-year variations in young shells was estimated by calculating the "Gleichläufigkeit" (Schweingruber, 1989) which is actually a sign-test. This test examines the number of similar growth rate changes (acceleration or deceleration) in two shells. It expresses the similarity as percentage of the total number of years that the two shells have in common. These percentages were averaged to obtain a measure of the similarity within and between any of the three clam samples.

A standardised growth index for young shells was obtained by comparing observed and expected growth for a certain year. Estimated expected growth in a particular year was defined as the average growth in 6 surrounding years. Measured growth was subtracted from estimated growth and the difference between expected and observed growth was then divided by the standard deviation of the (6-years) average (Witbaard, 1996). The resulting index value, which can be positive or negative, expresses the magnitude of the deviation. In this way a time series of index values was obtained for each shell. The index time series of the specimens in a sample of clams were averaged to obtain a mean chronology for the sample in question. These mean chronologies were correlated with each other to determine the level of synchrony between the separate samples. For a comparison between growth deviations and environmental data both the mean chronologies and individual index time series were used.

Growth increments in old shells, as in young shells, were transformed into a time series of index values expressing the deviation between observed and expected growth. In order to do so, first the strong correlation ($R_{average}$=0.86) between the (moving)

average increment widths and the corresponding standard deviations was eliminated by a logarithmic transformation of the increment widths. Because of the remaining ontogenetic trend of decreasing widths with age, expected growth was defined by a best-fitting (least squares) curve through the transformed increment widths. In all cases, a logarithmic curve turned out to be the most appropriate one. The required index (I_t) was obtained by $Log(I_t) = Log(R_t)-Log(G_t)$, and is zero when observed growth (R_t) equals expected growth (G_t), while it is positive or negative with an unbound maximum in case of a difference. For each of the separate measurements (27 old shells; 62 peels) a time series of index values was composed. These time series were subsequently averaged per sample giving rise to a mean chronology in which the common signal is enhanced and the noise cancelled out. The mean chronologies of the samples were correlated with each other to assess the synchrony. The coherence among the index time series was calculated with the mean correlation technique and in accordance with Cook & Kariukstis (1990) the following statistics were calculated:

- Average correlation between corresponding time intervals of all combinations of time series (R_{total}).
- Average correlation between corresponding time intervals of index series from different cross-sections of the same shell (R_{within}).
- Average correlation between corresponding time intervals of cross-sections of different shells ($R_{between}$).
- Effective correlation coefficient which incorporates the within and between cross-section signal. It takes the number of cross-sections per shell into account ($R_{effective}$).

The change in chronology coherence with increasing interval length was determined by recalculating the R-statistics after successive 10-year extensions of the time interval, *i.e.* 1991-1972, 1991-1962, 1991-1952 etc. All parameters have been calculated separately for each of the samples collected in 1983 (north and south) and the sample collected in 1991. On the basis of the correlation statistics the following quantities were derived (Cook & Kariukstis 1990):

- Expressed Population Signal (EPS). It expresses the variance which is explained by the common signal as fraction of the total variance in the chronology and is defined as; $EPS=R_{between}/(R_{between}+(1-R_{between})/n)$ with n= total number of shells and $R_{between}$ is substituted with $R_{effective}$ since more than one cross-section per shell was used.
- Signal to Noise Ratio (SNR). The SNR is a measure of the strength of the signal common in all shells and is calculated as $N*R_{between}/(1-R_{between})$.
- Chronology Standard Error (SE) is calculated as $1-R_{effective}/n$.
- Subsample Signal Strength (SSS). It is a measure which describes how well a subset of index time series describes the chronology of a larger set of index time series. It is

calculated as the quotient of EPS values of the subset and reference sample. The sample collected in 1983 was chosen as the subset of the chronology of north 1983+1991.

Figure 7.2

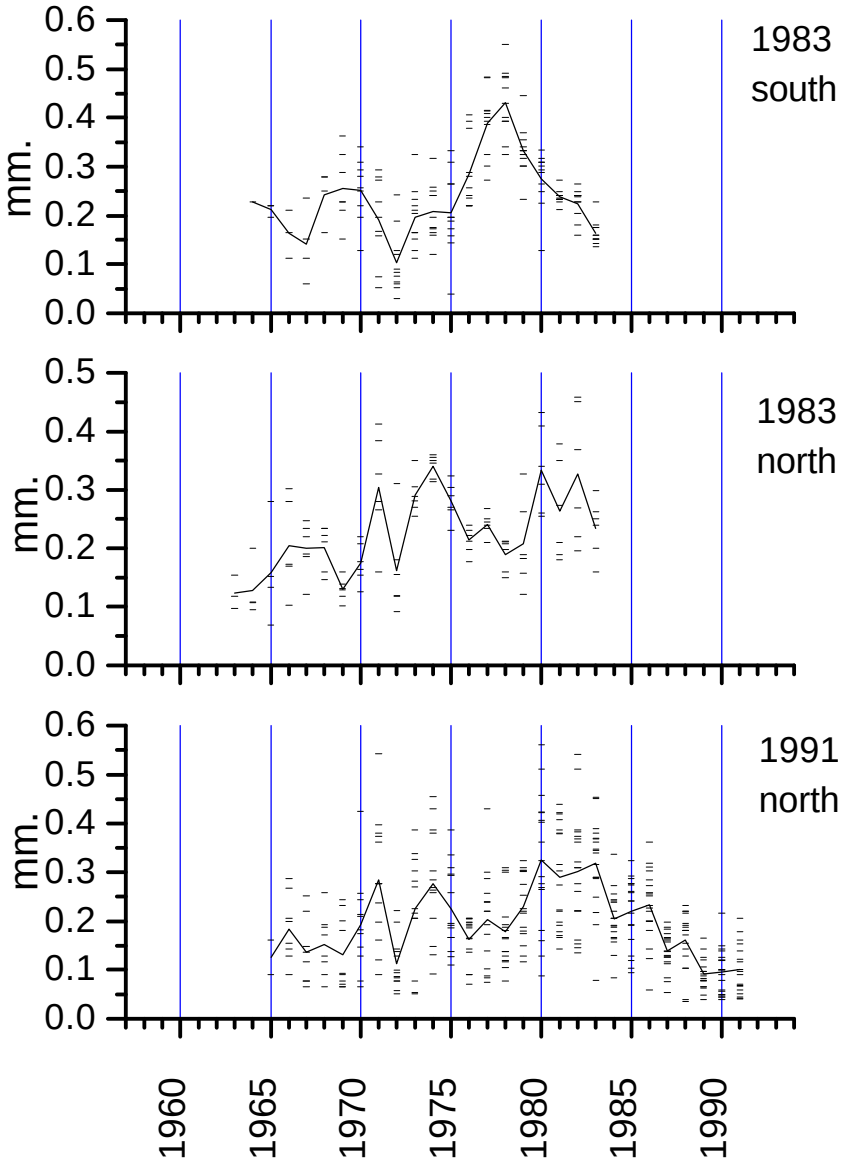

Figure 7.2. Temporal growth variations of young *Arctica* collected at the northern and southern locations in the Fladen Ground in 1983 and 1991. Each bar represents the increment width (mm) of one *Arctica* specimen. The lines connect the average increment width values of all clams in one sample.

RESULTS

Young shells

Figure 7.2 illustrates the variable widths of the hinge-band increments of young shells from both locations. Shells collected at the northern location (1983 and 1991) are characterised by a period of slow growth between 1976 and 1979 and a period of enhanced growth between 1980 and 1983. Shells from the southern site show the opposite trend of increasing widths since the early-1970s until 1978.

The percentage of shells with similar signed deviations for each year and the averaged individual index time series (mean chronology) of these young shells is depicted in figure 7.3a-c and in figure 7.3d-e. In some years (1966, 1969, 1975, 1976, 1978) 100% of the shells had equally signed deviations but these years are not always necessarily the ones with the largest deviation. Despite the opposite growth variations between north and south, growth was strongly depressed at both locations in 1972. Both the magnitude of deviation and percentage of shells was high.

Table 7.2

sample	South 1983	North 1983	North 1991
South 1983	0.78		
North 1983	0.53	0.79	
North 1991	0.50	0.67	0.60

Table 7.2. Average "Gleichläufigkeit" of the young shells sampled in 1983 and 1991. The values indicate the average fraction of synchronous growth variations.

The average similarity of growth variations between two shells, expressed as "Gleichläufigkeit", is given in table 7.2 and ranges between 0.50 and 0.79. The table illustrates that the similarity within a sample is much higher than that between different samples. A maximum "Gleichläufigkeit" value of 94% was found for two shells from the same boxcore collected in 1983.

The coefficient of correlation between the average index series (figure 7.3d-e) describes their similarity. For the 1983 and 1991 sample from the northern site a correlation of 0.83 ($n=13$; $p < 0.01$) was found. The correlation between north 1991 and south 1983 was almost zero whereas north 1983 and south 1983 were negatively correlated with a coefficient of -0.43.

Old shells

The mean chronologies (averaged index time series per sample) for the old shells in the samples south 1983, north 1983, north 1991 are given in figure 7.4a-c. In all samples one can discern an alternation of periods in which growth is either above or below the predicted values. In the chronologies from the northern site (figure 7.4b-c) the periods 1900-1915, 1937-1954 and 1979-1987 have predominantly positive (average) index values, while the intermediate periods have negative values. Except for the opposite trends since 1960, the long-term patterns of the northern and southern chronologies are very similar. Auto correlation indicates a 33-year-long cycle.

figure 7.3

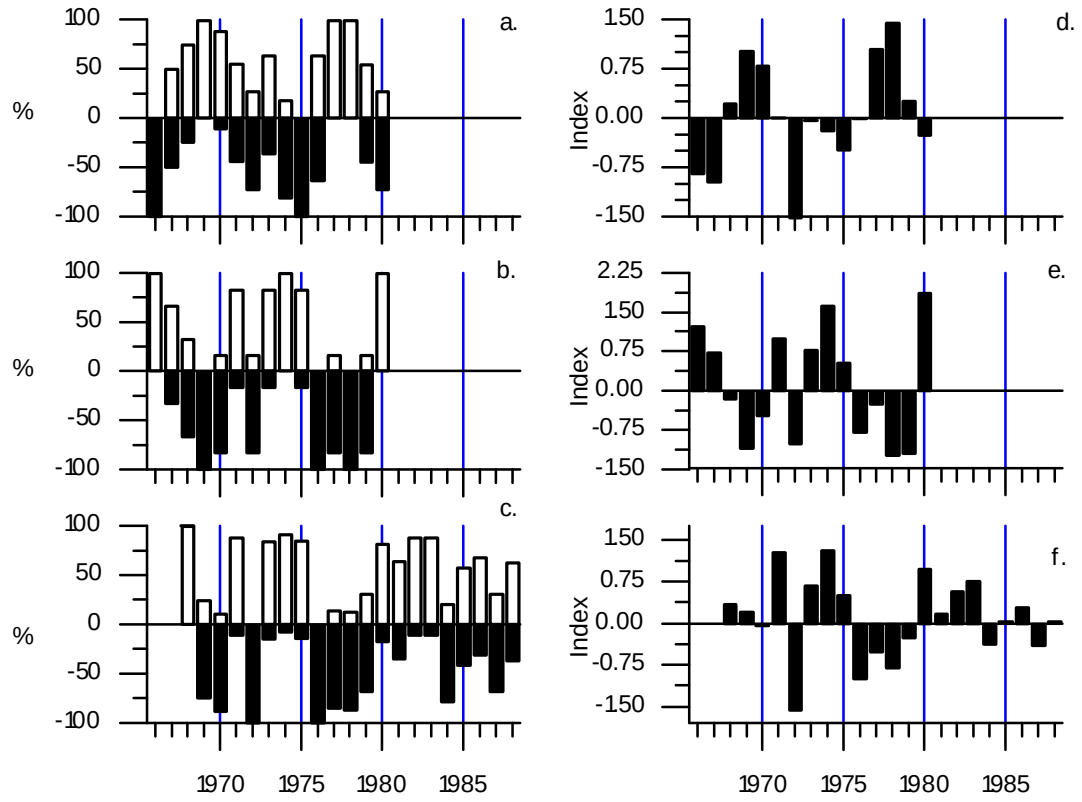

Figure 7.3. Event diagrams and magnitude of positive and negative growth deviations of young *Arctica* collected at south 1983 (a, d), north 1983 (b, e) and north 1991 (c, f). Figure (a-c), The percentage of specimens with similar signed growth deviations for subsequent years. (d-f), Mean index values calculated as deviation from 6 year mean.

The correlation between mean chronologies of north 1983 and north 1991 was 0.54. The coefficient of correlation between the northern chronology (1983+1991) and the southern one is 0.57. The correlation over the last 30 years is negative (R=-0.47), which is similar to that observed in the growth patterns of young shells.

There is also a good relation between the mean chronologies of young and old shells. The best correlation (R=0.79) was found for the shells from the southern site. The coefficient of correlation between mean chronologies derived from the young and old shells from the northern location varied between 0.42 and 0.64.

Figure 7.4

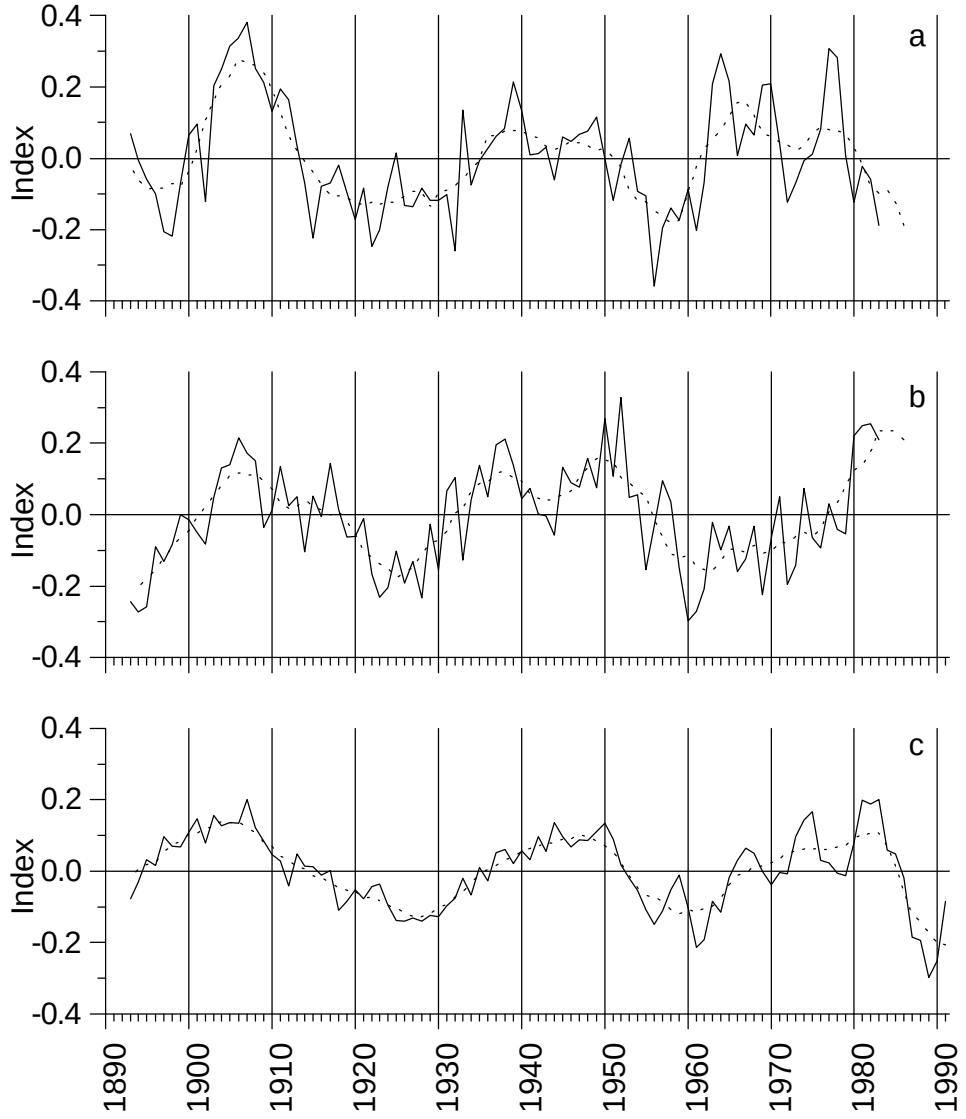

Figure 7.4. Mean chronologies of standardized growth variations in old shells from the Fladen Ground. Shown are the unsmoothed mean chronologies. The dotted lines represent the 3 year adjacent average. (a), South 1983, (b) North 1983 and (c) North 1991. Growth index on vertical axis.

Figure 7.5 illustrates the change of the Expressed Population Signal (EPS) and summarises the correlation statistics (table 7.3) which describe the coherence of the chronology, back in time. All samples except north 1983 have EPS values which

exceed the value of 0.85 which is an arbitrate value indicating an acceptable level of coherence in dendrochronology (Cook & Kariukstis, 1990). EPS of north 1991 stays close to this value for the complete length of the chronology while EPS of south 1983 drops below that value when the oldest section is included.

Figure 7.5

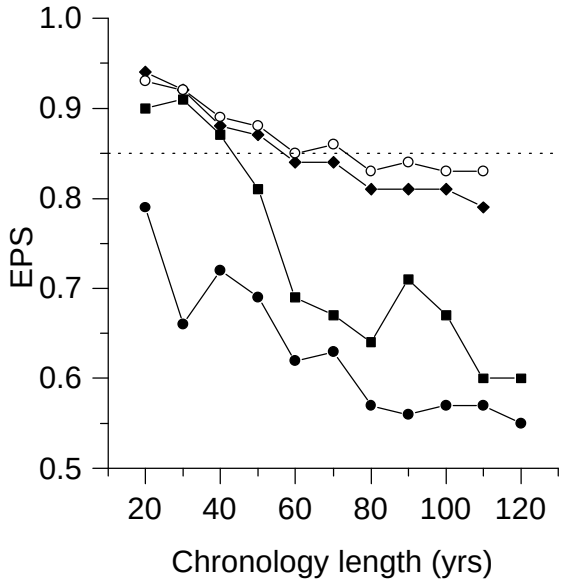

Figure 7.5. The dependence of the Expressed Population Signal (EPS) of chronology length for old shells. EPS values for unsmoothed chronologies. The dotted horizontal lined indicates an EPS value which is regarded as acceptable in dendrochronology. ■ south 1983; ● north 1983; ◆; north 1991; ❍ north 1983+1991.

SNR shows the same tendency with high values of SNR for the most recent sections and low values when the oldest sections are included (see table 7.3). The chronology of north 1991 has the highest SNR values, mainly due to the high number of shells. The Subsample Signal Strength (SSS) of north 1983, when considered as subset of the combined northern sample (1983+1991), is 0.69 for the period 1991-1892. This implies that by studying only 5 shells approximately 70% of the common signal of the entire chronology is found.

Correlation between chronologies and CPR-data

We correlated the individual time index series as well as the mean chronologies with both monthly and annual CPR phytoplankton data (area B2) *i.e.* the relative abundance of individual species of large dinoflagellates, large diatoms and the phytocolour index as well as their annual totals. Neither the mean chronologies of old nor young shells were significantly correlated with either annual phytocolour, annual

diatom abundance or annual dinoflagellate abundance or resulted in negative correlations (table 7.4). Only some combinations of the monthly abundance of certain diatoms or dinoflagellate species with some of the individual index time series were significantly correlated, but this might be due to chance. A pattern with high correlations in spring could not be discerned.

Period	R_{tot}	R_{with}	R_{betw}	R_{eff}	SNR	EPS	SE
				South 1983.			
1991-72	0.6	0.73	0.58	0.69	5.52	0.90	0.28
1991-62	0.59	0.67	0.57	0.71	5.3	0.91	0.27
1991-52	0.49	0.58	0.47	0.62	3.55	0.87	0.31
1991-42	0.35	0.42	0.34	0.51	2.06	0.81	0.35
1991-32	0.27	0.42	0.24	0.36	1.26	0.69	0.4
1991-22	0.25	0.40	0.22	0.34	1.13	0.67	0.41
1991-12	0.22	0.35	0.19	0.31	0.94	0.64	0.42
1991-02	0.26	0.37	0.24	0.38	1.26	0.71	0.39
1991-1892	0.22	0.30	0.20	0.34	1	0.67	0.41
1991-1882	0.17	0.23	0.15	0.27	0.71	0.6	0.43
				North 1983			
1991-72	0.42	0.74	0.38	0.43	3.06	0.79	0.34
1991-62	0.3	0.66	0.24	0.28	1.58	0.66	0.38
1991-52	0.31	0.54	0.27	0.34	1.85	0.72	0.36
1991-42	0.26	0.40	0.23	0.31	1.49	0.69	0.37
1991-32	0.21	0.39	0.18	0.25	1.1	0.62	0.39
1991-22	0.22	0.43	0.19	0.25	1.17	0.63	0.39
1991-12	0.18	0.37	0.15	0.21	0.88	0.57	0.40
1991-02	0.16	0.29	0.14	0.20	0.81	0.56	0.40
1991-1892	0.15	0.26	0.14	0.21	0.81	0.57	0.40
1991-1882	0.15	0.25	0.14	0.21	0.81	0.57	0.40
				North 1991			
1991-72	0.35	0.56	0.34	0.45	9.37	0.94	0.17
1991-62	0.3	0.53	0.29	0.39	7.41	0.92	0.18
1991-52	0.2	0.43	0.19	0.28	4.27	0.88	0.20
1991-42	0.19	0.39	0.18	0.28	4.03	0.87	0.20
1991-32	0.15	0.32	0.14	0.23	3.02	0.84	0.21
1991-22	0.14	0.30	0.13	0.22	2.79	0.84	0.21
1991-12	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-02	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-1892	0.12	0.27	0.11	0.19	2.33	0.81	0.21
1991-1882	0.11	0.27	0.10	0.18	2.09	0.79	0.21

Table 7.3. R-statistics and derived quantities describing the coherence between the individual time index series which were used to calculate the mean chronologies for the samples collected in 1991 and 1983

The results appeared to be better when the seventies were studied exclusively. During that period the mean chronologies showed some striking similarities with the CPR data. For the years 1971 to 1979 the mean chronology derived from young shells

from north 1991 yielded marginally significant correlations of 0.49 and 0.51 with phytocolour and total annual total diatom abundance, respectively.

DISCUSSION

Methodology

The high similarity of growth patterns in young shells, with 1972 as a recognisable year with strongly depressed growth, can be used to align or cross-date the chronologies from north 1983 and 1991. Results of this effort show that the excess number of growth increments in shells from 1991 as compared to those from 1983 equals the number of years which had passed since 1983 (figure 7.2). These data support the earlier findings of Witbaard *et al*. (1994) which indicate that growth increments in clams from both shallow and deeper waters are deposited annually. Furthermore, the high synchrony of growth variations in the shells from one locality suggests that a common environmental factor influenced the growth rate of different individuals in a similar way.

Table 7.4

Sample	Period	Diatoms	Dinoflag.	Phytocolour
young shells south 1983	1966-1980	0.16	0.16	0.26
young shells north 1983	1966-1980	-0.02	-0.17	-0.10
young shells north 1991	1968-1988	0.07	-0.21	0.05
old shells south 1983	1960-1983	-0.15	0.19	-0.23
old shells north 1983	1960-1983	-0.28	0.17	0.37
old shells north 1991	1960-1991	-0.33	-0.16	-0.35

Table 7.4. Correlation coefficients between the mean chronologies and indices of annual total abundance of large diatoms, dinoflagelates and phytocolour.

We checked the robustness of the time series that we obtained in two ways. Firstly, we applied alternative standardisation methods, *e.g.* the corridor-method (Cook & Kariukstis, 1990), which resulted in chronologies similar to the ones presented in this paper. Secondly, we constructed a large number of time series composed of randomly generated index values from which we calculated the statistical parameters listed in table 7.3. As these parameters were statistically insignificant for these randomly generated series, we concluded that our measured time series are unlikely a result of chance.

The lower correlation between old shells and the gradual deterioration of the chronology parameters (SNR, EPS; table 7.3) back in time, reflects the difficulty in

achieving an exact alignment of the yearly variations in old shells. This deficiency is ascribed to measurement errors due to the misinterpretation of rings or the presence of disturbance rings.

Our data, moreover, show the effect of sampling with a high spatial resolution. The 1983 boxcore samples show a high coherence compared to the 1991 sample which was collected with a beam trawl (see table 7.3). Compared to replicate boxcore samples from one position, a beam trawl covers a much larger area. This enhances the chance of including clams from sites with locally different sediment type or topography being factors which could affect food availability and growth (see Yager *et al*., 1993).

Environmental factors

The strong coherence among the index time series at one location and the spatial differences in growth between the two locations suggests the existence of a common environmental factor controlling shell growth, which varies over small spatial scales within the Fladen Ground.

As in many bivalves (Broom & Mason, 1978; Jones, *et al*., 1989), laboratory experiments with *Arctica* (chapter 4) reveal a clear correlation between temperature and growth. However, the year-to-year variations of the bottom water temperature in the Fladen Ground (Ellet & Blindheim, 1992) are so small that they can not explain the observed growth differences in young shells. This observation is supported by the lack of a positive correlation between local bottom water temperature and shell growth.

Another factor which directly affects growth rate is food availability. Its effect on *Arctica* growth can be easily demonstrated under experimental conditions (chapter 4), but determining the in-situ food availability, its variations and the effect on in-situ clam growth is more difficult. For this reason, we examined the relation between shell growth and phytoplankton standing stock derived from the CPR data (dinoflagellates, diatoms, phytocolour index; see table 7.4). However, few significant correlations were found.

One explanation for these poor correlations is the large difference in spatial resolution of both data sets (see Evans & Edwards, 1993). In the present study, we assessed the variability of food supply in the benthic boundary layer over an area of only a few km², while the CPR data consist of phytoplankton variables averaged over an area of thousands km². In view of the difference we found between growth variations of *Arctica* from the northern and southern locations, a strong correlation is not expected between the CPR data and local deviations in *Arctica* growth. This will only be the

case with a drastic alteration of the food web over the whole area, which can overshadow small-scale differences. In this respect, it is interesting to note some striking similarities between the mean chronologies of young shells and the CPR data during the 1970s. The extremely low growth in 1972 coincided with minimum diatom abundance, while the period with depressed growth between 1975 and 1980 was characterised by low diatom abundance and less intense phytoplankton blooms (Dickson *et al*., 1988b; Reid *et al*., 1990). During the 1970s marked changes in both weather and hydrographic conditions occurred in the northern North Sea. At this time, the "great salinity anomaly" (Dickson *et al*., 1988a; Turrell, 1992b) and a drastic reduction in the inflow of Atlantic water (Svendsen & Magnusson, 1992) took place in the northern North Sea. Corten & v.d Kamp (1992) regarded these changes as the most likely explanation for the concurrent changes in the stocks of several pelagic fish species (herring, sand eel, mackerel). Such large-scale events may also have caused the observed changes in the growth rate of *Arctica* at both sampling locations.

In view of recent hydrographical data published by Turrell (1992b) and Svendsen *et al*. (1991), it is likely that there exists a link between the growth of *Arctica* and the hydrographical regime in the Fladen Ground. The dense *Arctica* beds in the Fladen Ground lie in an area under the influence of a topographically steered eddy (Turrell, 1992a, b). The water circulation within this current system concentrates particles at its centre (Svendsen *et al*., 1991) and, consequently, affects the benthic food supply. Turrell (1992b) summarised evidence for the existence of the eddy in the area, *e.g.* the accumulation of fine sediments and the high chlorophyll content of these sediments. The final stationary positions of the drogue followed by Wilde *et al*. (1986) which led to the discovery of the two *Arctica* patches also points to the eddy system described by Turrell (1992a, b). According to Svendsen *et al*. (1991) the circulation over the Fladen Ground is coupled to the Atlantic inflow because parts of the Dooley Current (DC) and East Shetland Atlantic Inflow (ESAI) contribute to it (figure 7.1). Therefore, variations in these two currents may influence the strength of the eddy and, consequently, the accumulation of material in its centre. Hence annual variations in growth of *Arctica,* being the result of the eddy-mediated food supply, may reflect the variable inflow of Atlantic water into the northern North Sea.

We examined this hypothesis by comparing the growth variations of *Arctica* with data on the Atlantic inflow as estimated by Turrell (1992b) (*i.e*. on basis of wind direction and wind stress). The year-to-year variation in the wind driven component of the ESAI explains a significant part ($R=0.56$ $p<0.05$) of the growth variations observed in young animals from the northern location (figure 7.6).

Figure 7.6

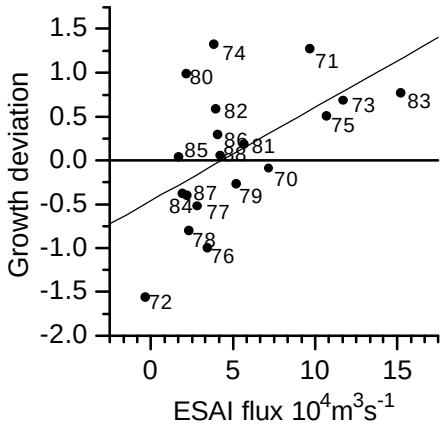

Figure 7.6. The correlation between the estimated East Shetland Atlantic Inflow (ESAI flux in $10^4m^3s^{-1}$; Turrell, 1992) and the magnitude of growth deviations (vertical axis) observed in young shells collected at the northern locations in 1991. (R=0.56, n=19, $p<0.05$). Numbers in graph indicate years.

Inflow into the northern North Sea is linked to the outflow along the Norwegian Trench (Dooley & Furnes, 1981; Reid *et al*., 1992). A stronger outflow is compensated by an increased inflow. Growth variations of *Arctica* should, according to our hypothesis, also correspond to the outflow along the trench. The relation between changes in the outflow (Furnes, 1992) and the mean chronology of *Arctica* growth from the northern location (1991+1983) is depicted in figure 7.7. The two datasets differ in details, *i.e.* maxima or minima do not coincide but the periodic alternation in both datasets have similar tendencies *i.e.* faster growth during periods of increased outflow and depressed growth during periods of reduced outflow along the Norwegian Trench. The estimated fluxes of Atlantic water into and out of the northern North Sea explain a significant part of both the long- and short-term growth variations of *Arctica*. It is therefore hypothesised that the underlying mechanism causing the variations in *Arctica* growth is the temporal variation in the strength of the topographically steered eddy.

A further extension of our hypotheses is that the (partly) opposing trends result from shifts in the position of the eddy. While the southern border of the eddy is determined by the 100 meter-depth contour its northward extension may be variable. As a result the bottom area, which is influenced by the eddy, might have had a variable position or dimension and consequently have favoured either the *Arctica* at the southern location, the *Arctica* from the northern location or both locations. Thus, a north-south movement of the area with increased deposition may explain the opposing growth

variations between north and south in recent years. The absence of opposing growth variations in the older chronology sections suggests that such conditions are exceptional and indicate that the Fladen Ground is, at least temporarily, less homogeneous than assumed previously.

Figure 7.7

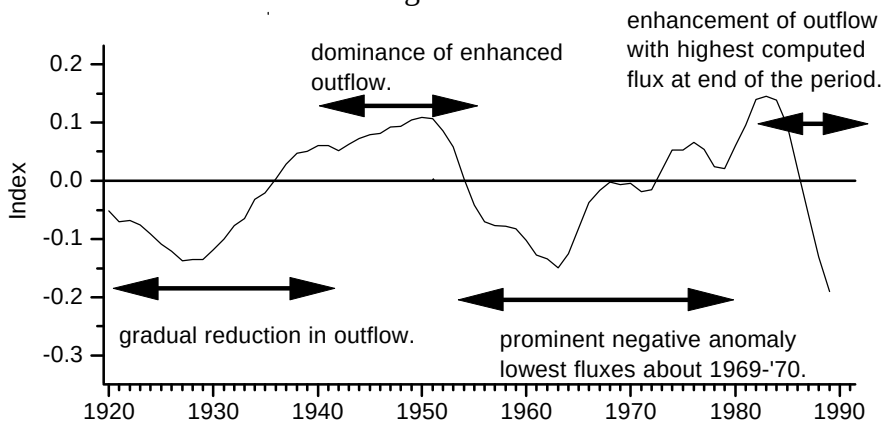

Figure 7.7. The tentative relation between the long-term mean chronology (north 1983+1991) with the estimated outflow along the Norwegian trench (Furnes, 1992).

The corresponding trends in the older chronology sections and changes reported for other regions suggest that the observed variations in shell growth of *Arctica* may be related to changes of a geographical scale larger than the Fladen Ground and which were not limited to most recent decades. Changing climatic conditions are often mentioned in such context (Aebisher *et al*., 1990; Dickson *et al*., 1988b).

The minimum index values in the early 1960s with their subsequent recovery concurred with the so called "gadoid outburst", the birth of exceptionally strong year classes of gadoid fishes (Cushing 1982), and coincided with a renewed and successful settlement of young *Arctica* in the Fladen Ground. Such successful settlement and recruitment were absent during the preceding 60 years as revealed by age structure analyses of the population. Conditions for juvenile survival or adult reproduction apparently improved since 1960.

There are other datasets as well which either demonstrate similar long-term trends or are characterised by obvious changes during similar periods. Austen *et al*. (1991) and Evans & Edwards (1993) observed changes in community structure of benthos and plankton respectively in the North Sea between 1979 and 1980, and our data likewise show such abrupt changes.

Similarities with other datasets are not limited to the most recent period. The increasing index values (figure 7.4) since the mid 1920s coincide with faunal changes in

the English Channel which is known as the "Russell cycle" (Cushing, 1982). Its main feature is the replacement of *Sagitta elegans* by *Sagitta setosa*, but also comprises the northward expansion of fish species with a southern origin between 1922 and 1950. During this period a predominance of Atlantic conditions in Arctic waters has also been observed (Blacker, 1957).

First signs of a reversal to the original fauna-composition in the English Channel were observed in the early 1960s and consisted of the reappearance of low densities of *S. elegans*, the changing abundance of non-clupeid fish larvae and the appearance of mackerel off Cornwall. In this period, shell growth indices also returned to their 1930 values. The more rapid return of the growth indice values of *Arctica* compared with the abundance change of the indicator species in the Channel is probably caused by the time it takes for these species to build a population with densities high enough to be sampled properly. These observations suggest that the underlying mechanism might have a North Sea wide extension and we assume hydrographical changes to be responsible. We thereby distinguish two periods in the chronology of growth variations of *Arctica*, a period comprising the years before 1960 during which the northern and the southern population have corresponding growth variations and a period after 1960 when the two populations have opposing growth trends. Thus even in putative stable regions like the Fladen Ground, the benthic environment can endure changes that generate heterogeneity on small spatial and temporal scales. Our observations stress the value of long-term growth studies for getting on track of events or mechanisms which control the functioning of the benthic community. Of course, studies like the present ones can only generate correlative evidence, actual multi disciplinary field studies are necessary to resolve the exact processes.

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